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Elevation gradient affects the distribution and host utilisation of *Zatypota anomala* (Hymenoptera, Ichneumonidae) associated with mesh web weaving spiders (Araneae, Dictynidae)

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Abstract

The spatial distribution of parasitoids is closely linked to the distribution and ecological requirements of their hosts. Several studies have documented changes in the fauna composition of parasitoids in response to elevation, but data on parasitoids associated with spiders are missing. The koinobiont ichneumonid wasp *Zatypota anomala* is strictly specialised on spiders of the genus *Dictyna* (Dictynidae) in Europe. We examined the distribution of spiders of the family Dictynidae in forest ecotones in central Europe across a broad elevation gradient (110–1466 m a.s.l.). We checked the spiders for parasitism by *Z. anomala*. It was most abundant at the mid-elevations (median 712 m a.s.l., range 179–870 m a.s.l.). We identified four dictynid spider species as *Z. anomala* hosts. These were *Dictyna arundinacea*, *Dictyna uncinata*, *Nigma flavescens*, and *Nigma walckenaeri*. All four species and the genus *Nigma* were recorded as hosts for the first time. The parasitoids

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strongly preferred juvenile instars of their hosts. The body length differed between parasitised *Dictyna* and *Nigma* spiders (medians: 1.95 mm and 2.55 mm, respectively). The distribution of *Dictyna* and *Nigma* spiders overlapped along the elevation gradient, but parasitism incidence significantly differed between spider genera along the elevation gradient. *Nigma* was parasitized at lower elevations between 179–254 m a.s.l. and *Dictyna* at higher elevations between 361–870 m a.s.l. The phenology of *Z. anomala* is closely tied to the univoltine life strategy of its host spiders. The parasitoid female oviposits in autumn, and its offspring overwinter as larvae on the host, reach adulthood during spring, and pass the summer as an adult.

Keywords

altitude, Darwin wasp, Ephialtini, host-parasitoid interaction, host range, host shift, host specificity, *Polysphincta* group of genera

Introduction

The effect of elevational gradient on species assemblages remains a central theme of biogeography and ecology (Körner 2007; Nogueira et al. 2021). Elevation effects on distribution ranges were well studied in both spiders (e.g., Chatzaki et al. 2005; Bowden and Buddle 2010; Foord and Dippenaar-Schoeman 2016; Mammola et al. 2021) and parasitoids (e.g., Péré et al. 2013; Corcos et al. 2018). Elevational gradients may occur within small geographical distances. Thus, they help assess community response to climate change and other environmental factors (Axmacher and Fiedler 2008; McCain 2009; Sundqvist et al. 2013; Chamberlain et al. 2016; Corcos et al. 2018). Published data on elevation effects on parasitoid richness and abundance appear to conflict in several studies (e.g., Veijalainen et al. 2014; Perillo et al. 2017); however, these conflicts might be resolvable if other ecological variables besides elevation are taken into consideration.

As some parasitoids may be specialised on hosts living at higher elevations, species-specific data are needed, particularly for associations where specific hosts are present at various elevations. Parasitism rates can differ with elevation and latitude (Virtanen and Neuvonen 1999; Hodkinson 2005). The meta-analysis by Péré et al. (2013) revealed that parasitism rates usually decrease as elevation increases. Some parasitoids use multiple hosts, including ichneumonid wasps, which we focus on here. Several studies have already quantified parasitoids associated with multiple hosts along elevation gradients (e.g., Hodkinson 2005; Corcos et al. 2018; Libra et al. 2019). However, studies of parasitoids associated with spiders which belong to the *Polysphincta* group of genera (usually called polysphinctines) are still missing.

Spiders of the family Dictynidae are aerial web builders producing 3D tangle webs on tree canopies, shrubs, or higher vegetation (Foelix 2011). Its genera, *Dictyna*, *Lathys*, and *Nigma*, are abundant in central Europe, share a similar ecological niche, and often co-exist in the canopy (e.g., Kůrka et al. 2015; CAS 2022; SARAS 2022). The only parasitoid that is known to be associated with Dictynidae is the here-studied *Zatypota anomala* (Holmgren) (Fitton et al. 1988). *Zatypota anomala*, distributed across the Holarctic, is known to be associated with Dictynidae – specifically, with the genus *Mallos* in North America (Vincent 1979) and with the genus *Dictyna* in Europe (Fitton

et al. 1988; Gauld and Dubois 2006; Miller et al. 2013; Korenko 2016). This wasp is also the only known parasitoid able to oviposit on cribellate spiders, whose webs contain hackled threads. This kind of silk requires the spider to comb the threads to a hackle (calamistrum), which are understood to attach and adhere to insects by van-der-Waals forces (Hawthorn and Opell 2002, 2003). The cribellate web is highly adhesive, attaches to prey, and deters attacks by predators and parasitoids (e.g., Foelix 2011).

In the present study, we aimed to explore elevation gradient effects on the parasitism of Dictynidae by the ichneumonid wasp parasitoid *Z. anomala*. We hypothesised that the composition of the dictynid spider community differs with elevation and that this may reflect elevation preferences in its parasitoid.

Materials and methods

Communities of spiders from the family Dictynidae (potential hosts of *Z. anomala*) were studied in 227 localities in 39 orographic units in Czechia and Slovakia at elevations ranging from 110 to 1466 m a.s.l. in the years 2016–2021 (Fig. 1). One to three samplings were performed at each locality. Spiders were collected by beating tree canopies (between 30 and 250 cm above the ground), with a square-shaped beating net (1-m^2 area) placed beneath. Parasitoid larvae were identified visually on spiders in the collected samples. The parasitised spiders were placed individually into tubes and

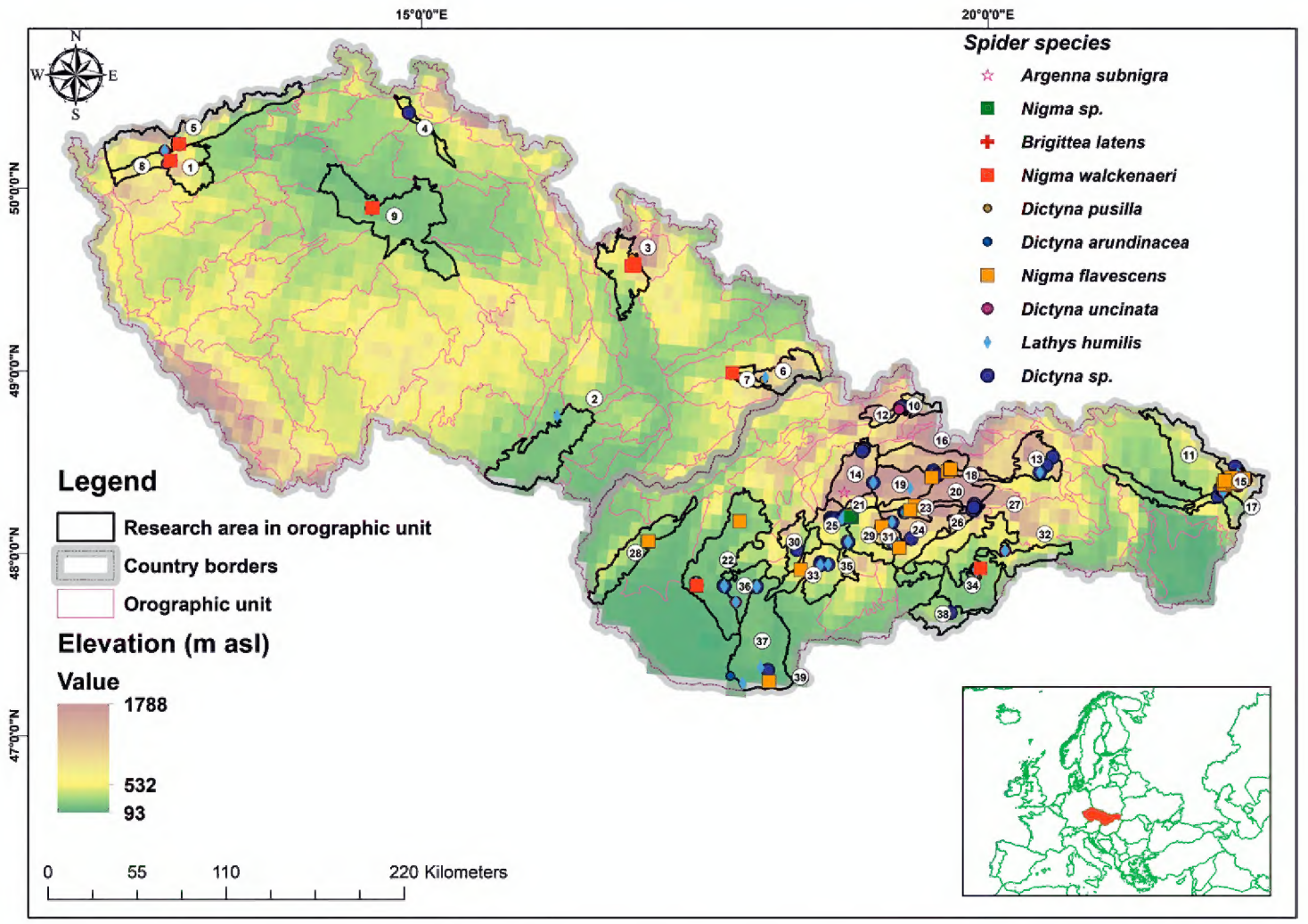

Figure 1. Map of studied localities and distributions of collected potential hosts (spiders of the family Dictynidae).

kept for wasp rearing and identification in the laboratory. Parasitised spiders that were not identified directly in the field were put in 70% ethanol together with unparasitised spiders, and all the collected individuals were analysed in detail in the laboratory. The parasitism rate was calculated as the sum of parasitized spiders relative to the number of examined spiders. Spiders were identified to species using Nentwig et al. (2022), and parasitoids were identified to species using Fitton et al. (1988) and Zwakhals (2006).

Statistical analyses

The two-tailed Kruskal-Wallis test and Dunn's multiple comparison test as Multiple Choice Test (MCT) were used to reveal differences in the distribution of dictynid species/genera along the elevation gradient. The two-tailed Mann-Whitney U test was used to reveal differences in the body size of parasitised dictynid spiders and differences in parasitoid distribution along the elevation gradient between those reared from *Dictyna* and *Nigma*. The calculations were performed in GraphPad InStat v. 3.06. Data are shown as medians and 1Q and 3Q of the Interquartile Range (IQR) unless stated otherwise.

We used the Arc GIS 10.3 environment for the spatial presentation of the association of the distribution of *Dictyna* and *Nigma* and their parasitoid *Z. anomala* with elevation. Part of the spatial analysis was dedicated to the distribution of host species and their parasitised specimens within the orographic units. Orographic units represent functional ecological units, each defined by elevation and by ecological, climatic, and geological conditions.

Results

Distribution of dictynid spider hosts

The examination of tree and shrub branches led to the collection of 2,332 individuals of dictynid spiders. They represented eight species that belonged to five genera, namely *Argenna*, *Brigittea*, *Dictyna*, *Lathys*, and *Nigma* (Table 1). Their distributions along the elevation

Table 1. Total number of collected dictynid spiders (potential hosts), their distribution along the elevation gradient, and parasitism by *Zatypota anomala*. Median and (1Q–3Q) of IQR are shown; data are presented in mm. N – number of collected spiders; p – number of parasitized spiders.

Spider species	N	Distribution	p
Argenna subnigra (O. P.-C.)	5	138(138–263)	0
Brigittea latens (Fabricius)	3	124(121–288)	0
Dictyna arundinacea (Linnaeus)	240	747(712–760)	5
Dictyna pusilla Thorell	61	870(870–870)	0
Dictyna uncinata Thorell	319	318(273–570)	14
Dictyna sp.	808	708 (439–760)	44
Lathys humilis (Blackwall)	742	572 (205–672)	0
Nigma flavescens (Walckenaer)	111	439(305–760)	1
Nigma walckenaeri (Roewer)	38	231(183–405)	8
Nigma sp.	5	431(431–441)	0
Total	2332	663(273–755)	72

gradient differed significantly among species (Kruskal-Wallis one-way ANOVA on ranks $H = 356$, $d_f = 7$, $p < .0001$, Table 2) and among genera (Kruskal-Wallis one-way ANOVA on ranks $H = 56$, $d_f = 2$, $p < .001$, Table 2). The genus *Dictyna* occurred at elevations with a median of 710 (361–760) m a.s.l. Its distribution differed significantly from *Lathys* and *Nigma*. *Nigma* preferred elevations with a median of 406 (288–754) m a.s.l., which was significantly lower than for *Dictyna* (MCT, $p < .01$, Table 2). *Lathys* was, like *Dictyna*, distributed across a relatively wide range of elevations, with a median of 572 (205–675) m a.s.l. that was significantly lower than that for *Dictina* (MCT, $p < .001$, Table 2). The rare species *Argenna subnigra* (O. Pickard-Cambridge) and *Brigittea latens* (Fabricius) were not included in the analyses because only five and three individuals were collected, respectively.

Table 2. Differences in elevation distribution between dictynid species and genera. Dunn's Multiply Comparisons Test. "z" means Mean Rand Differences. The rare species *A. subnigra* and *B. latens* were not included in the analysis. Spider individuals identified only to genus level were not included in the species analysis. The rare genera *Argenna* and *Brigittea* were not included in the genera analysis.

Comparison	*z*	*p*-value
Species		
D. arundinacea vs. *D. pusilla*	-287.87	< 0.001
D. arundinacea vs. *D. uncinata*	388.28	< 0.001
D. arundinacea vs. *L. humilis*	381.49	< 0.001
D. arundinacea vs. *N. flavescens*	250.46	< 0.001
D. arundinacea vs. *N. walckenaeri*	662.22	< 0.001
D. pusilla vs. *D. uncinata*	676.15	< 0.001
D. pusilla vs. *L. humilis*	669.36	< 0.001
D. pusilla vs. *N. flavescens*	538.34	< 0.001
D. pusilla vs. N. walckenaeri	950.09	< 0.001
D. uncinata vs. *L. humilis*	-6.788	ns
D. uncinata vs. *N. flavescens*	-137.82	ns
D. uncinata vs. *N. walckenaeri*	273.94	< 0.01
L. humilis vs. *N. flavescens*	-131.03	< 0.05
L. humilis vs. *N. walckenaeri*	280.72	< 0.01
N. flavescens vs. *N. walckenaeri*	411.75	< 0.001
Genera		
Dictyna vs. *Lathys*	192.87	< 0.001
Dictyna vs. *Nigma*	164.37	< 0.01
Lathys vs. *Nigma*	-28,50	ns

Host specificity and host trait preferences

Of the eight collected dictynid species, four species of spiders from the genera *Dictyna* and *Nigma* were documented as hosts (Table 1). All four spider species are documented as hosts of *Z. anomala* for the first time. Except for one adult spider female of *Dictyna uncinata*, all parasitised spiders (N = 72) were in the juvenile or subadult developmental stage. The average body length of the parasitised spider was 2.08 (1.92–2.60) mm. We found a significant difference in size between parasitized *Dictyna* (1.95 (1.83–2.09) mm) and *Nigma* spiders (2.55 (2.45–2.60) mm) (Mann-Whitney test, $U = 8.5$, $U' = 127.5$, $p < .001$). The body sizes of potential hosts (juvenile dictynid

Table 3. Body size of potential hosts and body size of parasitised spiders. Median and (1Q–3Q) of IQR are shown in mm. Different letters beside juvenile body sizes denote significant differences in body size analysed by Dunn's multiple comparison test.

	Dictyna	*Nigma*	*Lathys*
Female	2.55 (2.3–2.6)	3.0 (2.6–3.2)	2.45 (2.4–2.5)
Male	2.41 (2.3–2.5)	2.6 (2.51–2.73)	No data
Juvenile	1.92 (1.78–2.14)[b]	2.5 (2.3–2.7)[a]	2.0 (1.8–2.0)[b]
Parasitised	1.95 (1.84–2.09)	2.55 (2.45–2.6)	No record

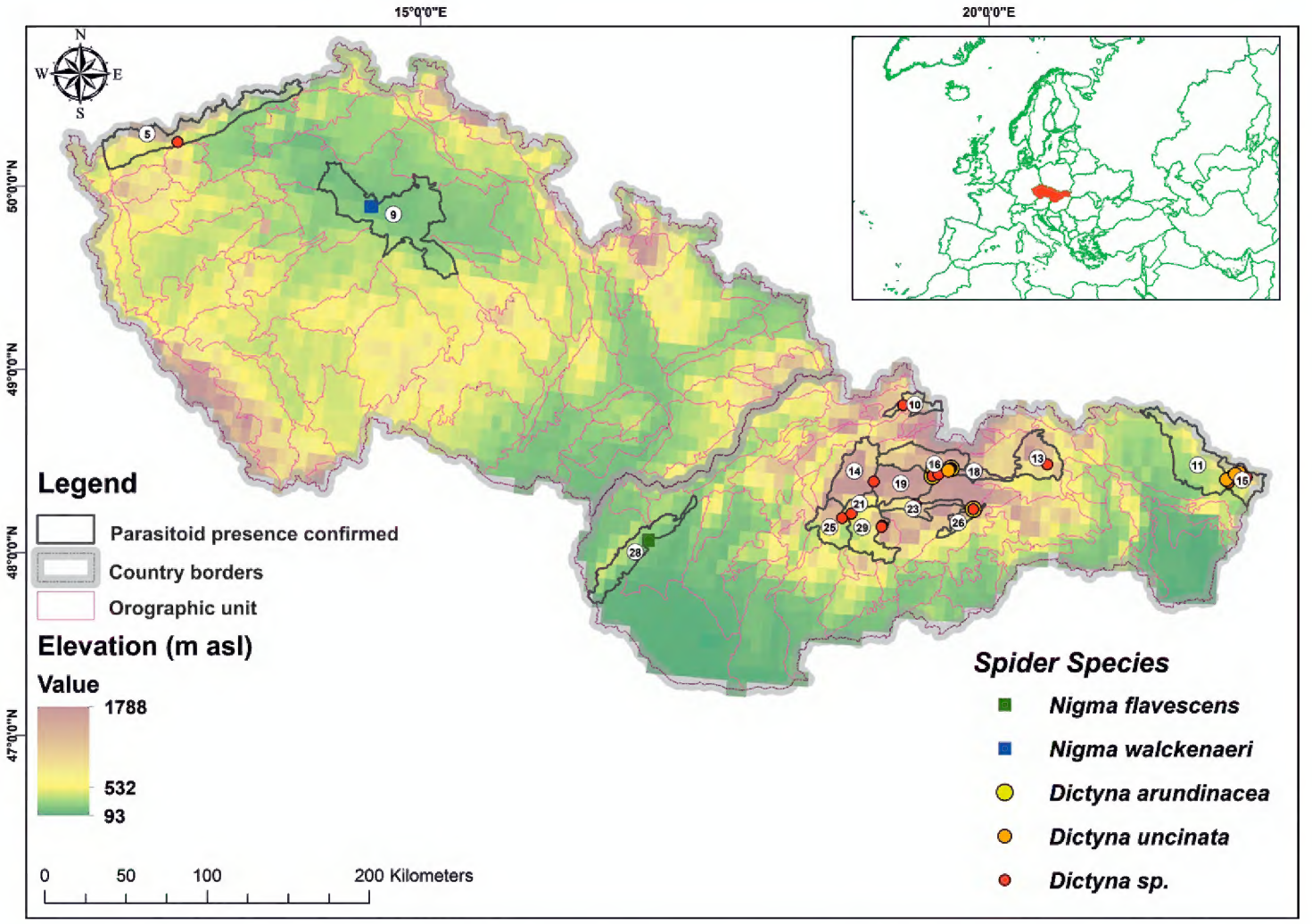

Figure 2. Map of the distribution of *Z. anomala* in association with different dictynid hosts.

spiders) differed among genera (Table 3); *Nigma* spiders were significantly larger than *Dictyna* and *Lathys* spiders (Kruskal-Wallis one-way ANOVA on ranks $H = 57$, $d_f = 2$, $p < .001$).

Host preferences change with elevation gradient

The parasitoid *Z. anomala* was present in 16 (33 localities) out of the 39 orographic units (227 localities) where accepted hosts (the genera *Nigma* and/or *Dictyna*) occurred in the examined spider community (Fig. 2). The parasitoid preferred sites with an intermediate elevation of 712 (486–765) m a.s.l. These elevations were inhabited by both accepted genera of spider hosts – specifically, by several species of the genus *Dictyna* and by *N. flavescens* (Fig. 2).

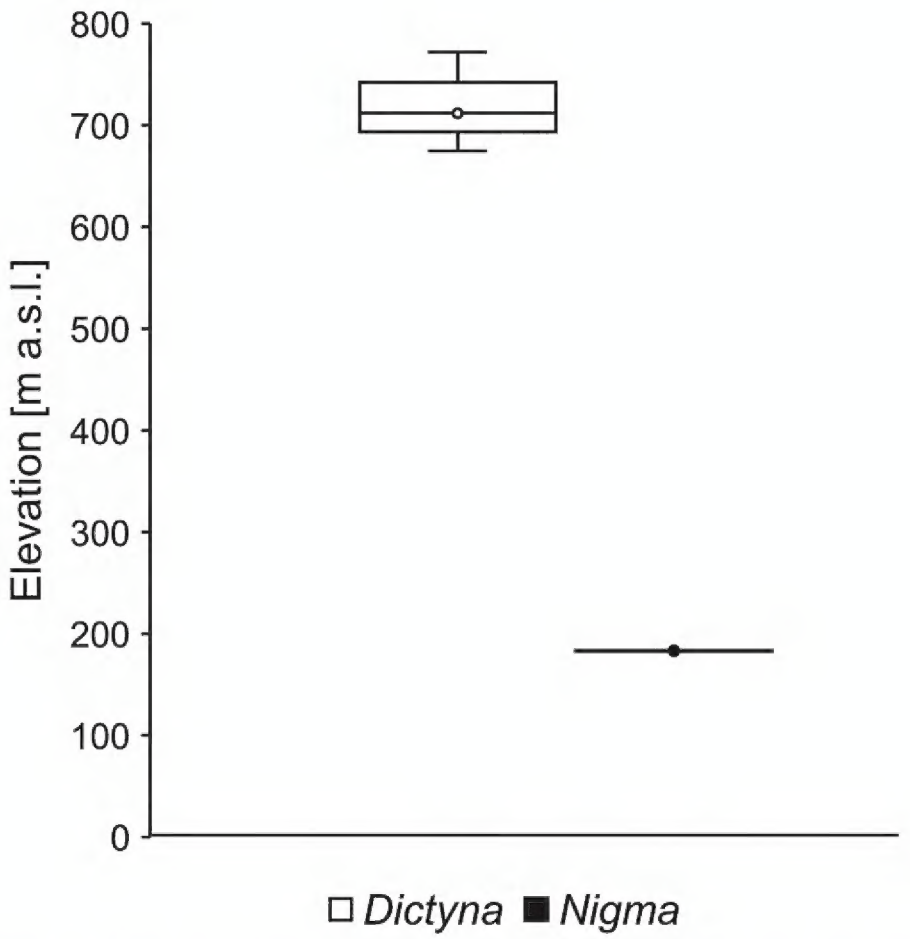

Figure 3. Differences in elevation where *Nigma* and *Dictyna* were parasitised. Bars and whiskers indicate median values, and Q1 and Q3 of IQR.

However, elevation differed significantly between localities where *Nigma* spp. were parasitised (183 (183–183) m a.s.l) and where *Dictyna* spp. were parasitized (712 (675–772) m a.s.l.) (Mann-Whitney test, $U = 0$, $U' = 567$, $p < .001$, Fig. 3). Parasitised *Nigma* spiders only occurred in three localities, and 70% of parasitised *Nigma* (N = 9) were collected in one locality at 183 m a.s.l.

Phenology

Dictynid spiders were parasitised by *Z. anomala* in high numbers in early spring and autumn. The parasitoid overwintered as larvae of the second instar and reached adulthood the following spring. Summer is expected to be the period of adult flight. Adult *Z. anomala* attacks the next generation of juvenile hosts in autumn, when the spiders have grown to a body size suitable for oviposition (Fig. 4). *Z. anomala* is thus univoltine and appears to be strictly dependent on the phenology of its dictynid hosts.

Discussion

Zatypota anomala presumably possess phenotypic plasticity, which enables it to attack spiders from different genera at different elevations. Although these accepted taxa differ in some morphological and behavioural traits, their ecological position in the local

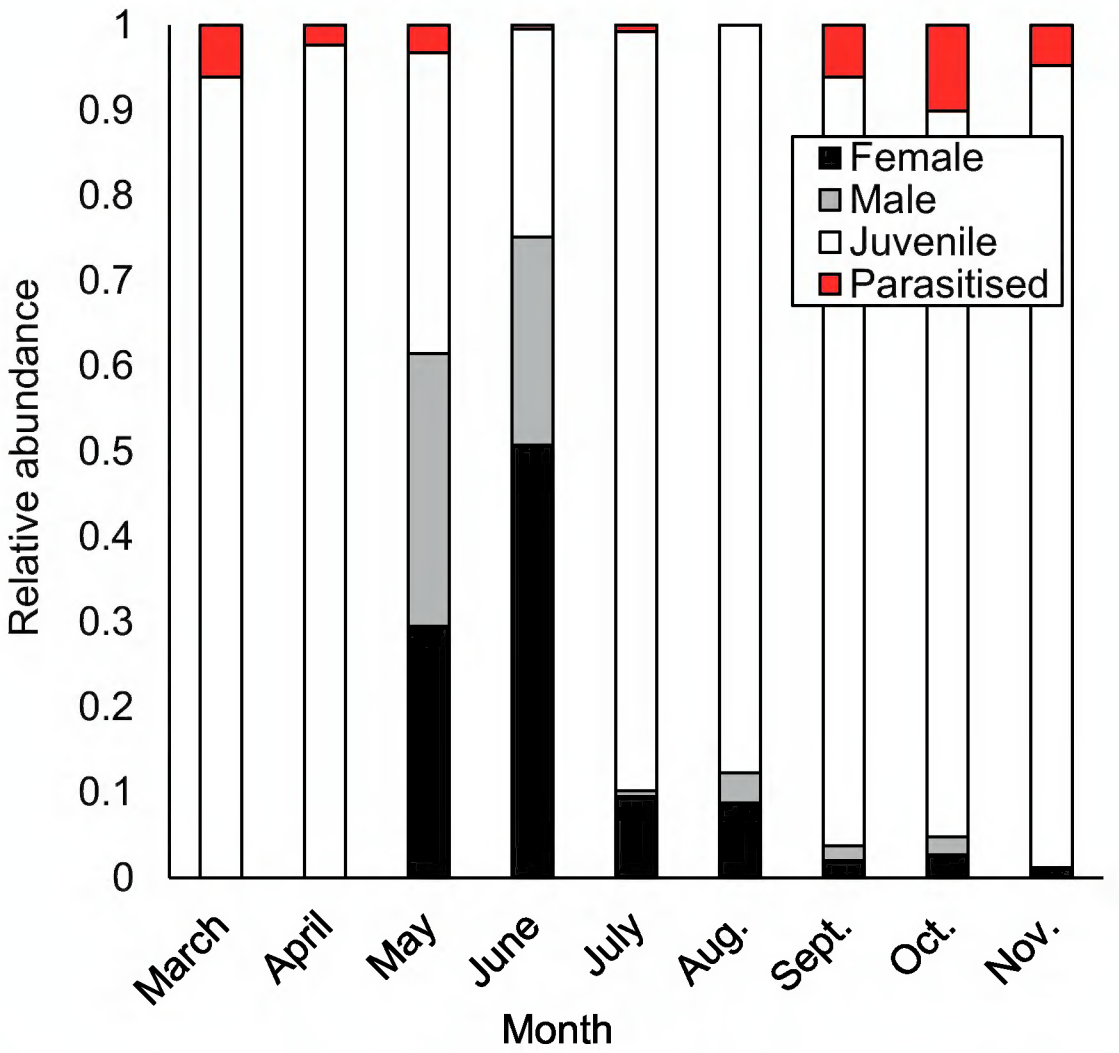

Figure 4. Seasonal occurrence of each developmental stage of dictynid hosts (genera *Dictyna* and *Nigma*) and parasitism incidence of *Z. anomala* in the years 2016–2021.

community is very similar across continents (e.g., Europe vs. North America) and along the elevation gradient. We found that *Z. anomala* attacked at least four species from the genera *Dictyna* and *Nigma*. Former host records of *Z. anomala* from Europe were mostly identified only to genus level as *Dictyna* spp.; only *Dictyna pusilla* Thorell was identified as a specific host species by Sedivy (1963) and Korenko (2017). Sparse records of hosts in North America include only the genera *Mallos* (Vincent 1979) and *Emblyna* (Howard 1888). It is interesting that several species of the genus *Dictyna* (including *D. arundinacea*, which is an accepted host in Europe) and one *Nigma* species are also present in North America (WSC 2022) but have not so far been recorded as hosts of *Z. anomala* there.

We found that *Z. anomala* accepted both *Dictyna* and *Nigma* spiders in Europe, but we never found both genera parasitised in the same locality. *Zatypota anomala* constantly attacked spider species which were highly abundant locally. Our results suggest that locally dominant dictynid species were easily available and consequently became preferred hosts. Local preference for the dominant host might also be imprinted onto the local population by hatching from the dominant host over several generations. In other parasitoids, it is known that offspring prefer to develop in/on the host in/on which their mother developed (Uller 2008; Stillwell and Fox 2009; Wolf and Wade 2009; Jones et al. 2015).

Polysphinctine wasps strictly associated with spiders possess high host specificity, even monophagy (e.g., Eberhard and Gonzaga 2019). *Zatypota anomala*, like some other

polysphinctine wasps, retains the ability to switch hosts within the group of closely-related spider taxa. We found that the host range of *Z. anomala* includes several genera across the Holarctic. In Europe, it attacks the ecologically similar genera *Dictyna* and *Nigma*. However, *Z. anomala* did not attack the ecologically similar and abundant genus *Lathys*. An explanation of this rejection of *Lathys* as host is still unavailable. Host size is of high importance for host acceptance by a parasitoid. *Zatypota anomala* parasitised spiders of the genus *Dictyna*, which are smaller than the parasitized *Nigma* species. In *Nigma*, only a few of the smallest individuals (below 2.70 mm) were parasitised, resembling in size the parasitised *Dictyna* spiders. The size of juvenile *Lathys* was very similar to that of parasitised *Dictyna* individuals, yet, the acceptance of spiders of the genus *Lathys* was not documented, despite the examination of 742 *Lathys* individuals. Thus, in this case, it appears that body size is not a sufficient reason for the parasitoid *Z. anomala* to avoid *Lathys*.

We found that *Z. anomala* preferred mid-elevations, around 700 m a.s.l., but we also found it in smaller numbers at lower elevations and not at all at higher elevations over 800 m a.s.l. *Zatypota anomala* is strictly associated with spiders from the family Dictynidae, which were rarely collected at elevations over 800 m a.s.l. The absence and low abundance of dictynid spiders in localities at higher elevations seem to indicate the upper limit of the parasitoid distribution on the elevation gradient. On the basis of the collected data, we assume the occurrence of host substitution in *Z. anomala*, where spiders of the genus *Dictyna* were parasitised in localities at middle elevations, and spiders of the genus *Nigma* were attacked in localities at lower elevations.

Parasitoid phenology is synchronised with host phenology. This synchronisation influences many traits of the parasitoid life history, including the number of generations per year (e.g., Godfray 1994). We found that *Zatypota anomala* is univoltine, and its phenology completely differs from that of *Z. percontatoria* and *Z. albicoxa*. Adult wasps emerge from overwintered juvenile or subadult dictynid spiders in the early spring, and flying female wasps must live until late summer and autumn, when dictynid spiders of the new generation grow to a suitable body size and females can successfully oviposit on them. In contrast, *Z. percontatoria* has several generations per year, since it accepts different host species that are available with a suitable body size at different times of the year. Therefore, the female can lay eggs on different hosts throughout most of the year (Korenko et al. 2016). *Zatypota albicoxa* (Walker) is also plurivoltine in Japan, having up to four generations annually due to the all-year availability of juvenile spiders (Tanaka 2007; Takasuka and Tanaka 2013).

The most important limitation on the acceptance of spider hosts by polysphinctines is the suitability of their size – specifically, the body size ratio between parasitoid and host (e.g., Korenko et al. 2011). *Zatypota anomala* prefers medium-sized juvenile spiders. However, the phenology of its spider hosts provides juvenile spiders of suitable body size for oviposition only in late summer and autumn. Therefore, females must overcome the hot summer period and oviposit when suitable spiders of the new generation become available. *Zatypota anomala* females are not documented to overwinter, so we suggest that females cannot oviposit on the spring spider population although there are juvenile spiders of suitable body length.

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